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RESEARCH ARTICLE

Activity of human motor system during action observation is modulated by object presence

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Abstract Neurons in the monkey mirror neuron system (MNS) become active when actions are observed or executed. Increases in activity are greater when objects are engaged than when the actions are mimed. This modulation occurs even when object manipulation is hidden from view. We examined whether human motor systems are similarly modulated during action observation because such observation-related modulations are potentially mediated by a putative human MNS. Transcranial magnetic stimulation (TMS) was used to elicit motor-evoked potentials (MEPs) of a grasping muscle while participants observed actual or pantomimed grasping movements whose endpoints were sometimes hidden from view. MEP amplitudes were found to be modulated by object presence. Critically, the object-based modulation was found when the participant directly observed object manipulation *and* when the object manipulation had to be inferred because it was hidden. These findings parallel studies of MNS activity in monkeys and support the hypothesis that the MNS influences motor system activity during action observation. Although the object-based modulation of MEP amplitudes was consistent with the hypotheses, the direction of the modulation was not—MEP amplitudes decreased during action observation in contrast to the increase that has previously been observed. We suggest that the decrease in MEP amplitude on object-present trials resulted from inhibitory mechanisms that were activated to suppress the observation-evoked response codes from generating overt muscle activity.

Keywords Action observation · Mirror neurons · Motor cortex · TMS

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Introduction

Studies of the firing patterns of neurons in ventral premotor (area F5) and the parietal areas of the macaque monkey cortex have shown that there is a subset of neurons that becomes active when actions are observed or executed (Fogassi et al. 2005; Gallese et al. 1996; Rizzolatti et al. 1996). These "mirror neurons" typically become active only during a meaningful interaction between an agent and an object and usually do not respond when the individual watches a hand mime an action, or only sees an object of interest (see Brass and Heyes 2005 and Rizzolatti and Craighero 2004; for recent reviews). Of particular relevance to the present study, Umilta et al. (2001) found that a subset of these neurons fired when monkeys observed the final stages of a grasp when the movements were directed to an object, but did not fire when the same movement was made without an object present. Critically, the object-dependent modulation occurred even when the grasp of the object was hidden by a screen, and the observer had to infer that the actor interacted with the object. Based on such findings, it has been suggested that mirror neurons in monkeys

code the effects of the action and aid in the recognition of actions and the intentions of the actor (e.g., Umilta et al. 2001).

Neuroimaging experiments suggest a similar mirror neuron system (MNS) may exist in humans. It has been reported that areas of the ventral premotor cortex (including Broca's area, a homologue of monkey F5, Petrides et al. 2005), parietal lobule, and others become active during both the observation and execution of action (Decety et al. 2002; Gazzola and Keysers 2009; Iacoboni et al. 1999; Mukamel et al. 2010). The meaning (Decety et al. 1997) and content (Buccino et al. 2001) of the observed actions seem to affect the patterns and levels of activation in the human brain. For example, Buccino et al. (2001) found that areas of the ventral premotor cortex and posterior parietal lobe were activated during the observation of hand actions with object (such as grasping a ball), but only the premotor areas were activated in a no-object condition in which the same actions were mimicked. Thus, additional areas were recruited when the hand actions involved objects than when these actions were mimicked. Similar to the conclusions drawn from the study of neural responses in the monkey cortex, it is thought that these observation-evoked activations represent a "motor resonance" in which observed actions activate representations of these actions in the observer (see Mukamel et al. 2010). These representations can then be used by the individual for a variety of social cognitive processes, including imitation, action and intention understanding, and observational learning (e.g., Buccino et al. 2001; see Rizzolatti and Craighero 2004 for a review).

Consistent with the notion that such an action observation system would be involved in facilitating imitation and observational learning of actions (i.e., the execution and/or learning of similar actions), numerous studies have revealed changes in corticospinal activity during action observation. Specifically, transcranial magnetic stimulation (TMS) studies of corticospinal excitability have revealed that the amplitudes of motor-evoked potentials (MEPs) increase when participants observe movements (e.g., Fadiga et al. 1995). This increase in excitation during action observation seems to be phase-dependent, in that the greatest increase in MEP amplitude occurs when that specific muscle would be contracting during actual task performance (Gangitano et al. 2001). Because a number of the cortical areas that are activated during action observation (most notably the premotor cortex) project directly and indirectly to lower motor neurons of the spinal cord, the specific origin of these observation-evoked modulations in MEP amplitude cannot be definitively determined using TMS alone. The bulk of the evidence thus far, however, suggests that a key source of the modulation in corticospinal excitability that occurs during action observation is the primary motor cortex (M1) (Baldissera et al. 2001; Hari et al. 1998; Strafella and Paus 2000). Thus, it is generally concluded that the changes in MEP amplitude observed during action observation occur because activation of the putative human MNS (i.e., premotor and parietal areas) subsequently generates a representation of the observed movement in M1 via cortico–cortico connections (e.g., Strafella and Paus 2000; see Fadiga et al. 2005 for a review).

Although these TMS experiments suggest that the modulation of corticospinal activity is generally consistent with the patterns of mirror neuron activation during action observation in non-human primates and neuroimaging studies in humans, it has yet to be tested whether these object-dependent modulations in corticospinal activity (e.g., Fadiga et al. 1995) occur in conditions in which object interaction has to be inferred because the object interaction is not seen (Umilta et al. 2001). If, as hypothesized, humans have a MNS that responds and functions in a manner consistent with the firing properties of mirror neurons in the monkey and the activations in this MNS subsequently influence corticospinal activity, then alterations in corticospinal activity during action observation should be present when the actor interacts with an object. Of particular interest to the present study, however, are the potential modulations that occur when object interaction is not directly observed because it is hidden from view (e.g., Umilta et al. 2001). This unseen modulation is of specific interest because it would support the hypothesis that the observation-evoked representations are coded with respect to the goals of the actor, not simply the movement trajectories. Such a result would be consistent with the finding of increased recruitment of parietal areas during object-oriented relative to mimed actions (Buccino et al. 2001). As a consequence, such a result would also support the hypothesized role of the action observation system in coding and understanding the goals and intentions of the actor (Buccino et al. 2001; Umilta et al. 2001) and its subsequent influence on the motor system.

The present study was designed to determine whether the activation of the human motor system during action observation is dependent on object interaction and, importantly, whether it occurs even when the endpoint of the movement and the object interaction is hidden from view. To this end, the methods of Umilta et al. (2001) were adapted for a human TMS study. TMS was delivered over the thumb area in M1 at three main time points during the observation of a grasp: rest, transport, and grasp. Participants watched four videos during the study. The hand picked up an apple in two videos. In the other two videos, the hand mimed the movement and grasped empty space. In one object-present video and one object-absent video, the action was completed in full view (Full Vision condition).

In the other videos, a screen moved into view after the participant saw whether an object was present or not. The screen prevented the participant from seeing the real or mimed grasp (Partial Vision condition). It was hypothesized that if the modulation in the excitability of the human motor system during action observation is object-dependent, but not vision-dependent, then MEP amplitudes would be modulated by the presence of the object in both Full and Partial Vision conditions. Because previous studies have revealed object-dependent modulation of corticospinal activity (e.g., Fadiga et al. 1995), the critical and novel comparison of the present study was between object-present and object-absent conditions in the Partial Vision condition. In contrast, if the modulation of corticospinal activation only occurs when the observer actually witnesses object interaction, then MEP amplitude will only be modulated by object presence in the Full Vision condition.

Methods

Participants

There were twelve participants (5 women, 7 men) from the University of Calgary community (20–29 years). Prior to participation, each participant completed and signed a medical questionnaire, a short-form adaptation of a handedness questionnaire (seven questions from the Waterloo Handedness Questionnaire, Bryden 1977), and an informed consent form. All volunteers were right-handed (reporting right hand preference for at least 6 of the 7 items) and had normal or corrected-to-normal vision. They were financially compensated for their time. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki. The University of Calgary Conjoint Health Research Ethics Board approved all procedures.

Procedure and apparatus

Each participant was tested separately in a single session of 60–90 min. Participants sat approximately 1 m from a table and watched videos displayed on a 19″ LCD monitor placed on the table. Their eyes were at the same height as the center of the monitor. Participants kept their forearms on their lap, with the thumb and the fingers of the right arm free to move. They were told to remain motionless and as relaxed as possible during the study.

Electromyography (EMG) electrodes were positioned on the skin (shaved and cleaned with 70% alcohol tissue) of the right arm over the flexor pollicis brevis (FPB) and the flexor digitorum superficialis (FDS). EMG signals from both FPB and FDS were monitored by an experimenter on a 19” monitor outside of the view of the participant. Participants were reminded to “relax” at the beginning of each part of the mapping procedure and at the beginning of each block of trials. Participants were also reminded to “relax” whenever muscle activity was detected during testing, but such instances were rare. Although the exact number of reminders “to relax” were not recorded, the number of reminders during the mapping procedure was much greater than during the experimental phase, because participants generally obeyed these instructions during testing.

TMS pulses were delivered using a Magstim 200 stimulator (Carmarthenshire, Wales, UK) with a figure-eight coil (diameter wings of 70 mm). MEPs were recorded from the FPB and FDS after a single TMS pulse was administered to the M1 of the hemisphere contralateral to the test limb (left hemisphere). FPB was the target muscle for the study because of its primary role in grasping actions. FDS was recorded as a secondary muscle and was monitored to ensure that the participants remained relaxed (muscles at rest) and were not overtly imitating the actions during testing. Because FPB was the muscle of primary interest in the present study, mapping and threshold procedures were completed for the FPB. For this reason, FDS MEPs were not consistently observed (within and across participants) and were not analyzed.

The optimal scalp position for FPB stimulation was found using conventional procedures. A point, 2 cm anterior and 6 cm lateral to the vertex, was identified. The coil was placed over this spot and oriented at an angle of 45° to the midline and tangential to the scalp. The coil was systematically moved around this point, and stimuli were delivered (with increasing levels of stimulator output in a stepwise manner) until stable MEPs in the FPB were observed. Once this “hot spot” was located, the stimulator output was adjusted until the resting motor threshold (rMT) was identified—the minimum stimulator output that elicited MEPs with at least 100 μV (peak-to-peak) from the FPB on 5 of 10 stimulations. This position was then marked on the scalp with a non-permanent marker to aid in coil repositioning. Throughout the mapping and threshold procedure, participants fixated a black cross in the middle of the white background on the monitor.

Custom LabView software recorded a window of EMG data (sampled at a rate of 4,000 Hz) from 100 ms before to 1,500 ms after the TMS pulse. Data were cleaned and examined offline using a separate custom LabView program. EMG signals from the FPB and FDS were amplified and filtered (bandwidth 20–450 Hz) using a Delsys Bagnoli-8 system.

Task

Each trial consisted of the delivery of a single TMS pulse during a video clip showing a right hand performing a

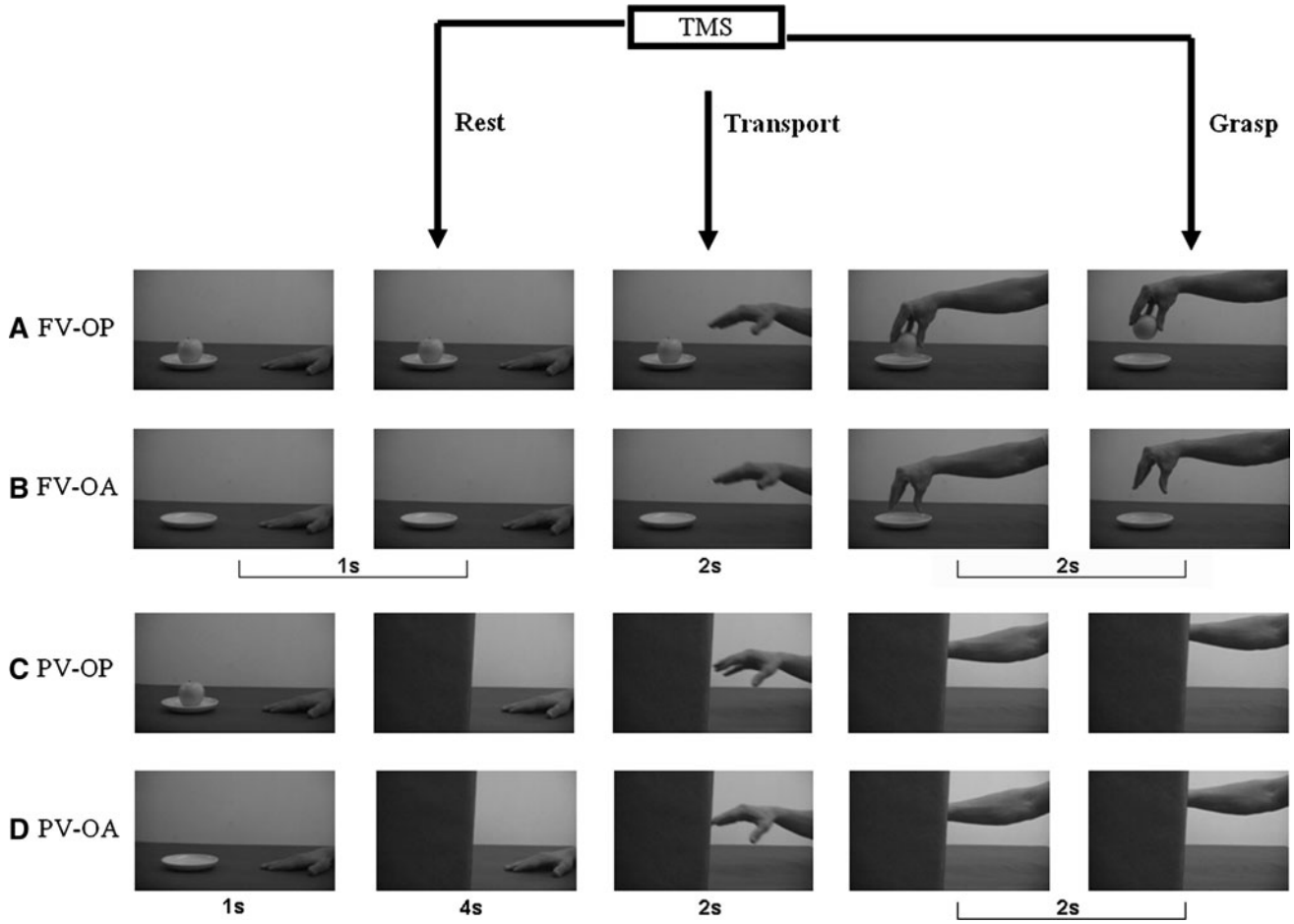

Fig. 1 Depiction of the four videos and the points of the video where TMS was delivered. **a** FV-OP: Full Vision Object-Present. **b** FV-OA: Full Vision Object-Absent. **c** PV-OP: Partial Vision Object-Present. **d** PV-OA: Partial Vision Object-Absent. Note that the time information underneath the pictures shows the approximate times for the events—see text for more detail

reach-to-and-grasp action over a plate. Videos began with a view of a white plate (with or without an apple) and a hand lying flat on a red table. The 4 videos consisted of a factorial combination of two Vision and two Object conditions (Fig. 1). The Vision conditions were as follows: Full Vision—participant saw the whole movement; and Partial Vision—part of the transport and the whole grasp phase of the movement was covered by a screen. The Object conditions were as follows: Object-Present—a green apple was present and was grasped; and Object-Absent—the plate was empty.

In Full Vision videos, the hand remained at rest for the first 1 s then moved toward the plate for 2 s, and then grasped and lifted the apple (if present) for 2 s. In Partial Vision videos, participants saw the plate (and the apple, if present) and the hand at rest for 1 s. A solid red screen then slid from the left side to cover the left half of the table including the plate. The movement of the screen took approximately 2 s to complete. Two seconds after the screen acquired its final position, the hand started moving and went behind the screen to complete the actual or mimed action. Across all videos, the hand moved from rest to form a grasping posture at approximately 1 s (midpoint between the start and the object location), reached the object location by 2 s, grasped or mimed a grasping action at 3 s, and then lifted the object (or mimed the lifting action) for the remaining 1 s. Although each video consisted of different movements, we ensured that the timing and kinematics of the actions were as consistent across trials as possible by recording and analyzing a number of clips in each condition and selecting the clips that were the most similar.

Thus, in the Full Vision Object-Present condition (Fig. 1a), participants saw the hand move and then grasp, and lift an apple. In the Partial Vision Object-Present condition (Fig. 1c), participants saw that an apple was present before a screen covered the left half of the scene. After the screen was placed, the hand reached behind the screen and picked up the apple. Participants had to infer object-grasp and lift because this was not seen (but the upper arm was seen to pause during the grasp phase and then elevate

during the lift phase). In the Full Vision Object-Absent condition (Fig. 1b), there was no apple on the plate and the hand mimed the reach-to-grasp-and-lift movement when it reached the empty plate. Finally, in the Partial Vision Object-Absent condition (Fig. 1d), there was no apple on the plate and the hand mimed the reach-to-grasp-and-lift movement behind the screen. The four videos were shown in separate blocks. Block order was randomized for each participant.

A TMS pulse (115% rMT) was delivered at one of four different time points during the videos. The "rest" stimulation occurred when the hand was on the table (approximately 0.5 s from the start of the Full Vision videos and 4.3 s from the start of the Partial Vision videos, when the screen had finished moving into view and just before the hand started moving). The timing of the "rest" TMS pulse coincided with the video frame that was the midpoint between start of the "rest" and the start of "transport" phases. The "transport" stimulation occurred at the spatial midpoint of the transport component of the arm movement (for the Partial Vision conditions, this occurred just before the hand moved behind the screen). The "grasp" stimulation occurred 1 s after the grasp and the object had been lifted. Finally, the "end" stimulation occurred 0.5 s after the hand had stopped the lifting motion. There were 15 rest, 15 transport, 15 grasp, and 5 end trials per block. The end trials were catch trials used to decrease the chance of participants altering cortical excitability on the grasp trials because they could anticipate the coming TMS stimulus. The data for end trials were discarded. The 50 trials were presented in a random order.

Data reduction and analysis

For the analysis, peak-to-peak MEP amplitudes for FPB were computed as the difference between the positive and negative peaks (measured in μV), which were recorded during a time window that was approximately 20–80 ms after TMS delivery. The analysis window was individually set for each participant, to ensure accurate analysis of the MEPs by accounting for between-participant variability in the timing of the MEPs, and ensuring that non-MEP-related signals were not analyzed. The time window of analysis for each participant was identified using the following procedure. A mean MEP trace was created by averaging all EMG recordings across the data collection session for that individual into a single trace. An interactive analysis program was then used to identify the window of analysis by placing markers at the key points along the mean trace (i.e., at MEP onset and at the first zero-crossing during the silent period). The analysis program then analyzed the EMG (MEPs) from each trial and recorded the difference between the positive and negative peak values within the time window identified from that mean trace. This procedure is identical to that used in previous work (e.g., Carson et al. 2005).

Prior to statistical analysis, outliers were eliminated from the data. Individual MEP amplitudes were eliminated when the background EMG during a time window from 85 ms before the TMS pulse to 5 ms before the TMS pulse was three standard deviations larger than the individual's mean background EMG. Individual MEP amplitudes were also rejected if the peak-to-peak MEP amplitude was greater than 3 standard deviations larger than the mean MEP amplitude for an individual condition. Less than 2% of the data were rejected.

Results

Based on previous studies of the firing patterns of neurons in the monkey cortex that have mirror properties (e.g., Umilta et al. 2001), we predicted that MEP amplitudes on Object-Present trials would be different from those on Object-Absent trials in both the Full and Partial Vision conditions. Further, based on previous TMS results showing a phase-dependent (Gangitano et al. 2001) modulation in humans, we predicted that these differences in MEP amplitude may be apparent during the transport (preparation to grasp) and grasping phases of the movement, but not during the rest phase. To test these predictions, mean peak-to-peak MEP amplitudes for FPB were submitted to a 2 (Object: Object-Present, Object-Absent) by 2 (Vision Condition: Full, Partial) by 3 (Action Phase: Rest, Transport, Grasp) repeated-measures ANOVA. The only significant effect from this analysis was a main effect for Object, $F(1,11) = 5.38$, $p < 0.05$. Interestingly, the analysis revealed that MEP amplitudes in the Object-Present (1529 μV) were significantly lower than in the Object-Absent condition (1967 μV).

Although the predicted 3-way interaction between Vision Condition, Object, and Action Phase was not significant ($F < 1.0$), we chose to analyze the interaction using Tukey's *HSD*[1] because: (1) we had specific predictions

[1] Note that these specific comparisons were also statistically tested using a series of planned comparisons using one-tailed *t* tests ($p < 0.05$). The results of the secondary planned comparison analysis were consistent with the main Tukey's *HSD* analysis reported here—MEP amplitudes on Object-Present trials were different from those on Object-Absent trials during the grasp and transport phases, but not rest phase, in both Full and Partial Vision conditions. Although a series of planned *t* test comparisons is a more conventional method for conducting such planned comparisons, we chose to report the results of the more conservative Tukey's *HSD* test. We chose to report the more conservative test as the main analysis because: (1) the observed pattern of differences was in the opposite direction to what was predicted and what has been observed in previous studies; and (2) we were conducting a post hoc test of a non-significant interaction.

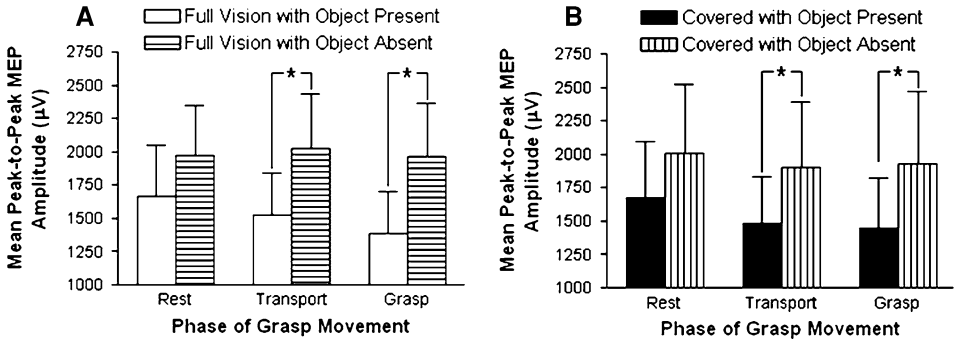

Fig. 2 Mean motor-evoked potential amplitude (μV) as a function of object presence and grasp phase for the **a** Full Vision and the **b** Partial Vision condition. SEM *bars* are shown. Comparisons marked with an asterisks indicate significant differences (Tukey's *HSD*, $p < 0.05$)

about significant differences between MEP amplitudes across specific conditions; and (2) an examination of the interaction alone would not provide the most sensitive test of these predictions. The absence or presence of the interaction does not provide the most sensitive testing because a significant interaction would only reveal that there are significant differences between the differences of the different conditions. It would not necessarily reveal that there were (or were not) significant differences between individual conditions. Consistent with this line of reasoning and with predictions, post hoc analysis of the 3-way interaction revealed significant differences in the MEP amplitudes in the Object-Present and Object-Absent conditions in the transport and grasping phases ($p < 0.05$), but not in the rest phase ($p > 0.05$). It is important to note that this pattern of differences was observed in both the Full and Partial Vision conditions (Fig. 2a, b).

Discussion

Overall, the pattern of effects observed in the present study was consistent with our predictions based on studies of the activity in the monkey (Umilta et al. 2001) and putative human MNS (e.g., Buccino et al. 2001), showing that activity in these networks of cortical neurons during action observation is modulated by object interaction. These data suggest that the goal-directed nature of the observed action is a key factor in determining the response of the action observation system and subsequent activation of the corticospinal system (see also Cattaneo et al. 2009). Of critical importance, this is the first known TMS study to show modulation of the human corticospinal tract when object interaction had to be inferred because the goal-directed object interaction was hidden from view. Thus, the data support the hypothesized role of the action observation system in coding and understanding the goals and intentions of the observed actor.

While the predicted pattern of significant differences emerged, the observed direction of the modulation was not consistent with previous TMS literature. Specifically, MEP amplitudes were significantly lower in the Object-Present than in the Object-Absent conditions (Fig. 2), suggesting that there was an inhibitory effect of object manipulation on the activity of M1 during action observation. This decrease in MEP amplitude during action observation is in contrast to other studies reporting an increase in MEP amplitude during action observation (e.g., Fadiga et al. 1995; Gangitano et al. 2001). Studies of the influence of action-related sentences on the excitability of the corticospinal tract, however, have observed inhibitory influences (e.g., Buccino et al. 2005; see below for more detail). In addition, other recent work from our laboratory on individual differences in the excitability of the corticospinal tract during action observation revealed a subgroup of participants who demonstrated a null to an inhibitory response (Ray 2009). The present report is the first, to our knowledge, of a significant inhibitory effect of action observation on the human corticospinal system (but see Baldissera et al. (2001) for a report of inhibitory effects in H-reflex magnitude during action observation).

The exact nature of this inhibitory influence is unclear. We suggest, however, that it was the result of an inhibitory process that participants enacted in an attempt to remain at rest during action observation, as they were instructed and reminded to do. That is, to keep muscles quiescent and prevent overt imitative movement, participants may have activated an inhibitory process to combat any excitatory influence from the putative MNS that occurred as the result of witnessed or inferred object interaction. Such an inhibitory process has been proposed to be an important part of the motor system (Howard and Tipper 1997; Sohn and Hallett 2004; Welsh and Elliott 2004) and has recently been suggested to be an important component of the overall neural response during action observation (Brass and Heyes 2005). In the specific context of action observation, it has been suggested that such a controlled inhibitory process would allow individuals to selectively imitate only certain observed actions, by preventing unwanted observation-evoked response codes from surpassing the threshold for overt action (Brass and Heyes 2005; van Leeuwen et al. 2009). Although the present study may be the first to

observe a marker of this inhibitory process in the activity of the corticospinal tract in humans during action observation, Kraskov et al. (2009) reported that a subset of pyramidal tract neurons originating in Area F5 of 2 macaques with "mirror-like" firing patterns demonstrated a *decrease* in firing rate during action observation. Likewise, Gazzola and Keysers (2009) reported that, whereas areas associated with the putative human MNS (e.g., ventral premotor and parietal areas) showed the typical increase in activity while participants watched videos of hand movements, the activity in M1 appeared to decrease. Consistent with the proposal of Brass and Heyes (2005) and others, Gazzola and Keysers (2009) and Kraskov et al. (2009) suggested that the suppression of pyramidal neuron firing and M1 activity may reflect mechanisms that are activated to inhibit overt movement during action observation.

It is further suggested here that the magnitude of the inhibitory process activated during action observation in the present study was dependent on the strength of the observation-evoked response codes. In the Object-Absent conditions, where there was a weak observation-evoked response code (or no response code at all), little or no inhibition was needed to suppress the activation and the motor system remained at a baseline state. In contrast, because the observed object-based actions in the Object-Present condition were so salient, a stronger representation of the action was evoked throughout a wider cortical network (i.e., premotor and parietal versus premotor areas alone; Buccino et al. 2001). In response to this high level of excitation, participants attempted to remain at rest by engaging a stronger inhibitory process, which worked on the motor system to counteract the excitatory influences from the action observation system, and prevent the response codes subsequently activated in the motor system from reaching excitation of sufficient amplitude to cause muscle activity. It might have been that participants overestimated the amount of inhibition necessary to prevent the excitatory influences of action observation from generating overt action. This overestimation caused an overall inhibitory balance in the motor system and excitation dropped to below baseline levels, leading to smaller amplitude MEPs during the critical phases of the observed movement.

Although it is likely that this inhibitory influence originates from frontal areas such as dorsolateral prefrontal cortex (Ford et al. 2005), it is possible that some other areas associated with executive control may also play a role. Consistent with the hypothesized role of executive function in the control of an inhibitory mechanism during imitation, van Leeuwen et al. (2009) recently showed that imitative actions were facilitated when participants are engaged in a secondary memory task. Presumably, the facilitation of the imitative movements occurred because the executive-controlled inhibitory mechanism was "distracted" during the performance of the secondary task, allowing more of the automatically activated excitatory processes to facilitate the planning and execution of the observed action (see Chandrasekharan et al. 2006).

It is also interesting to note that the decreases in excitability were present in both the transport and grasping phases of the action. The modulation of the excitability of the FPB representation would be expected in the grasp phase, because the FPB would be maximally activated while holding the object against gravity. The modulation in activity during transport could have occurred for two reasons. First, FPB excitability could be modulated in anticipation of force generated during the grasp phase. If the action observation system is involved in the understanding and the anticipation of what another person is doing, and generating predictions about the observed action, then modulations during the transport phase could reflect the activity associated with the anticipation of force exerted during the grasp.[2] Second, the modulation could have occurred because the hand is starting to close as it approaches the object. While it is unclear which of these possible processes contributed most to the modulation in the transport phase, these data are generally consistent with previous work showing modulation of the cortical representation of muscles involved in the grasping action prior to the actual grasp (Gangitano et al. 2001).

Finally, as noted earlier in the Discussion, research on the role of the motor system in language processing, stemming from embodied theories of language and cognition,

[2] Although the present study was motivated by previous neurophysiological research, it should be noted that the anticipatory and inferred modulation of the corticospinal tract is also broadly consistent with theoretical accounts of the processes of action observation, imitation, and joint action based on ideomotor theory (e.g., Prinz 2005; Sebanz and Knoblich 2009). According to ideomotor theory, action plans and their associated effects on the environment are tightly linked and maintained in a common representation (Hommel et al. 2001; Prinz 1997). The critical implication of this proposed common coding system for the present discussion is that, because action plans and effects are tightly linked in these common representations, it is possible that the perception (actual, imagined, or inferred) of a goal-directed action effect (e.g., the grasp and lifting of an apple) can automatically activate the motor plan associated with that effect. Thus, the pattern of corticospinal modulation observed here may have occurred because the anticipation and perception (Full Vision condition) or imagination/visualization (Partial Vision condition) of the grasp and lift activated the grasping plan in the motor system and, subsequently, the inhibitory mechanism preventing overt imitation. Because investigations of the cortical areas involved in ideomotor coding is in its early stages of development and has focused exclusively on single person action execution contexts (i.e., the research has not directly addressed action observation—Elsner et al. 2002; Melcher et al. 2008), it is unclear at this point how compatible the ideomotor account is with the neurophysiological research that motivated the present study. However, it is clear that, on the conceptual level, the pattern of effects observed in the present study is congruent with the ideomotor account of action observation and joint action.

has revealed both facilitatory and inhibitory effects of action words on the motor system (e.g., Buccino et al. 2005; de Vega et al. 2004; Oliveri et al. 2004; Scorolli and Borghi 2007).[3] A recent model (Chersi et al. 2010) has been developed in an attempt to account for these seemingly discordant patterns of effects. An extensive review of the model is beyond the scope of the present paper. The relevant aspects of the model for the present discussion, however, are that the discordant facilitatory and inhibitory effects may be accounted for by the time course of inhibitory and facilitatory mechanisms working on chains of action representations that are spread throughout the parietal and motor systems. Specifically, it was proposed that the processing of action words involves the activation of chained action representations. This action code activation is thought to occur in a manner that is similar to the action code activation that is considered to be engaged during action observation. It was further proposed that the specific direction (i.e., inhibitory or facilitatory) of the observed influence of the action word is dependent upon the timing of the TMS pulse (in neurophysiological studies) or the "go" signal (in behavioral studies). The transition from inhibitory to facilitatory effects occurs because of the dynamics of the neurons in the pools representing the actions. The initial (up to 500 ms poststimulus) period of inhibitory or interference effects is proposed to be a reflection of an early, and temporary, reduction in the firing rates of the neurons in the chained action representations. The later (roughly 500–1,000 ms poststimulus) period of facilitation effects is thought to be a reflection of enhanced firing rates in these neural pools (see Chersi et al. 2010 for more specific detail).

It is unclear whether a similar time course approach could account for the differences in the findings of the present study and those of previous work in action observation—the inhibitory effects were observed in both critical time points in the present study, and the timing of TMS delivery was similar to that in previous studies showing facilitatory effects (e.g., Gangitano et al. 2001). Instead, the purpose of presenting a brief review of the literature on motor system activation during language processing is to highlight the broader conclusion that the seemingly discordant effects observed in these studies may be due to two different manifestations of the same underlying neural events; namely the activation of action representations by the reception of action-related words. In this way, seemingly discordant effects may in fact have common neural substrates and the manifestation of these effects will be dependent on a number of factors such as task instructions and demands, and the timing of the stimuli (see Chersi et al. 2010 and Papeo et al. 2009; for more details). This conclusion is broadly consistent with the point of view presented here.

In sum, the main result of the present study was that the pattern of the object-dependent changes in the excitability of the human motor system was consistent with the firing patterns of neurons in the monkey MNS. Specifically, there were differences in the amplitude of the MEPs evoked during Object-Present and Object-Absent conditions. Critically, the object- and phase-dependent modulation of the motor system occurred when the participants observed *and* inferred object interaction (Umilta et al. 2001). These findings are consistent with the hypothesized role a putative human MNS may play in imitation and intention understanding, because the modulation was detected only when the actions were associated with a distinct purpose, whether that purpose was directly observed or not. Interestingly, the changes in corticospinal activation were inhibitory in nature. These inhibitory effects are suggested to represent the engagement of an inhibitory process, hypothesized to prevent excessive and unwanted imitation (Brass and Heyes 2005; van Leeuwen et al. 2009). The source of this inhibitory influence, and the conditions under which it is modulated, remains unclear and requires further investigation.

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